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POPULATION ANALYSIS AND PRODUCTION APPROACH: TWO TRENDS IN AQUATIC ECOLOGY

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ABSTRACT. In current aquatic ecology, one can discern two main research programs: production-energetic and population-analytical ones. Within the framework of production-energetic program, it is usually assumed that elements of ecosystem are connected by rather tough system of functional relations, and therefore knowing the values of some measurable variables, one can predict those of other variables which, though being important, are not easy to evaluate. Such predictions imply the existence of ecological constants or a system of stable ratios. This can be named the nomothetic paradigm. Another paradigm of the same research program is the comparative-typological one treating the transfer of some ecological values from one ecosystem to others (e. g. in the case of calculating the regression equation for group of lakes). This approach deals with averaged (for some time) ecological values and considers the trophic levels as basic elements of interaction. Population-analytical program searches for explanations of particular situations rather than for general descriptive laws. Only methods of such analysis are supposed to be universal. Population analysis aimes: 1. to study the processes rather than averaged states of population; 2. to use temporal scale that agrees with the rates of main processes; 3. to reveal the whole chain of causes and effects that determine the population change under changing environmental conditions; 4. to study the specific responses of population attributes to the influence of certain factors.

Key words: population analysis, production approach, research program, aquatic ecosystem, ecological law.

There are two research programs co-existing in current ecology as a whole and in aquatic ecology (hydrobiology) in particular, namely *production-energetic* and *population-analytic* ones. The discussion of their content in various aspects and from different points of view may be found in several works (e.g. Winberg 1981, Rigler 1982, Ghilarov 1988, 1992). The aim of the present paper is to consider in general terms these programs outlining their most characteristic questions as well as the limits of their applicability.

To begin with, let us imagine that we come to the lake shore, and we want to understand, how the ecosystem of this lake functions. What shall we do to obtain the answer? (Note that such a way of the question statement reflects the core of research program). One may discern here two different approaches, two outlooks, or even two visions of the world. The first one assumes that there exists rather a tough system of functional relations between elements of an ecosystem and/or between attributes of these elements, and, having measured a few of these attributes (input variables), we will be able to calculate all other variables. The problem is to reveal these relations, to search for ecological invariants or constants, i.e. the components usually included in the laws in "exact" or "hard" sciences. This way of thinking is apparently quite traditional for natural sciences.

Within the frameworks of the second approach, one does not usually assume the existence of some general laws or universal regularities in relations between ecological variables (though in fact they are not neglected). Ecologists inclined to this approach try to elaborate the certain research program aimed at understanding the mechanism of particular system functioning. There are three key notions here: the research program, the mechanism of functioning, and the particular system. The emphasis on the *particular system* should underline that different systems are considered here as far less similar to each other and much more variable in space and time than they are treated in the frameworks of the former approach. *The mechanism of functioning* is the combination of relations within a system and also between the system elements and the environment. In

contrast to a law, as it is treated in physics, this combination lacks the universal character but relates to particular situation, particular lake (or other water body), and particular space or time. But the essence of this approach is the *research program*. Suggested to be universal, i.e. to be applicable to different systems, this program combines some rules, methods, and modes of research activity targeted to elucidation of the mechanism of particular ecosystem functioning.

In aquatic ecology, the former trend of reseach is realized in the production-energetic or, as it was earlier named in Russian literature, "balance approach" (Rossolimo 1934). The aim of the balance approach is to calculate a biotic budget of community, i.e. to establish absolute values and quantitative relations between separate pathways of energy flow within one and the same trophic level as well as between successive trophic levels, to find regular patterns of biotic budgets, and to reveal general quantitative dependences providing the calculation of such budgets.

The energy flow is usually characterized, according to this approach, by the production value of a trophic level or some other group of individuals within a biotic community. Other characteristics used are the food ingestion (or consumption, C), assimilated energy of food or simply assimilation (A), and expenses to maintain vital functions ("metabolic expenses", T). The system of ecological ratios ("efficiencies") includes: assimilation efficiency (a) — the ratio of assimilation to ingestion at the same trophic level; energy coefficient of growth of the first order by Ivlev (K_2), or gross efficiency of growth by Richman (see Kozlovsky 1968) — the ratio of production to ingestion at the same level; energy coefficient of growth of the second order by Ivlev (K_2), or net efficiency of growth by Richman (see Kozlovsky 1968) — the ratio of production to assimilation at the same level; ecological efficiency — the ratio between productions of successive trophic levels. Mean numeric values of these coefficients have been established and are widely used for calculations, i.e. assimilation efficiency is assumed to be 0.6 or 0.8, K_2 ranges from 0.2 to 0.4, ecological efficiency is about 10 %.

There are many ways of using this set of coefficients for working out a biotic balance. For instance, based on the values of assimilation efficiency (a), production efficiency (K_2), and ecological efficiency (i.e. using all the complex of independent coefficients, as $K_1 = \alpha K_2$), and having determined an input variable, namely production, assimilation or food intake at some trophic level, one may easily calculate all other elements of biotic balance. Thus if one assumes the primary production to be an input variable, the production of subsequent trophic levels may be obtained from the value of ecological efficiency; having known the production, the assimilation may be found by K_2; the food ingestion may be calculated according to a priori accepted assimilation efficiency; and the metabolic expenses may be found as the difference between the assimilation and production.

A more common variant of calculations is not relied upon the a priori known values of production and ecological efficiency but use the known dependence of metabolism (the rate of oxygen consumption) on the body weights of individuals. Knowing the mean weight of individuals, one may calculate their metabolism, and then, using the equation $P = \frac{K_2}{1 - K_1} T$, one may find the production; the sum of production and metabolic expenses allows to obtain the assimilation, and the food intake may be calculated from the values of assimilation and assimilation efficiency.

Another possibility to use the balance approach leads to the search for relations between production characteristics at non-adjacent trophic levels, e.g. between the primary production and the catch of fish (Buljon and Winberg 1981), or between functional (production-energetic) and structural (species diversity) characteristics of a community (Alimov 1989).

It is evident that in all its applications the balance approach is based on the belief in existence of ecological constants or, that is the same, stable ratios between ecological characteristics ("ecological laws"). As in physics, the constants and laws are here the attributes of one and the same picture of the world which is well arranged and, using Nalimov's (1983) expression "pulled on the constants".

This belief in constants and laws is the central paradigm of the balance approach being included in the core of its research program. We combine here the notion of paradigm, introduced by Kuhn (1970), with the notion of research program, according to Lakatos (1970). It may be briefly designated as *nomothetic* paradigm ("nomos" — the law). In frameworks of this paradigm, the ecological laws are searched for as various regression functions measuring the mean expectation of one variable relative to the other meanwhile the coefficients of these dependences are just the constants sought for.

For example, equations and coefficients obtained for data on different lakes may be applied for estimation of some ecological characteristics of those lakes which have not been

included in the initial set of points. Thus ecological characteristics of some lakes (ecosystems) are transferred to other lakes (ecosystems). Presumably, just this approach was considered by Winberg (1985) as "traditional comparative-typological thinking of a limnologist". Therefore, the second paradigm of the core may be named "*comparative-typological*" or the paradigm of ecosystem similarity.

Besides these central paradigms of balance ("production-energetic") approach, we may indicate several minor paradigms or "auxiliary hypotheses" comprising the "protective belt" of given research program if one uses Lakatos' (1970) terms. The first hypothesis of this protective belt is the possibility to resolve a community into trophic levels, though this resolution is never reduced up to the level of separate populations. This hypothesis of trophic levels traced throughout all the history of the balance approach (Winberg 1936, 1981, 1983) may be briefly characterized by Winberg's (1983) words: "In relation to matter cycles and productivity, the really interacting elements of an ecosystem are not species populations but functionally united groups of them".

The second "auxiliary hypothesis" considers the attributes of a community or an ecosystem as averaged for long time interval (growing season, year). Seasonal dynamics of processes occured in the ecosystem is in fact ignored by this hypothesis, aptly named by Vilenkin (1978) as "energetics in average".

It is clear that all these attributes of balance approach are closely interrelated, and the auxiliary hypotheses serve as a support for paradigms of the core. Nevertheless, one may ask if it is possible to reduce the balance pattern to the level of separate populations, i. e. to develop a matrix of energy and matter flows between separate populations? And is it impossible to calculate a budget for separate short intervals of time and to follow its seasonal dynamics without the averaging? Principally, both things are possible but only at cost of refusal of the methodology of balance approach with its nomothetic and comparative paradigms. Actually, the system of interspecific relations and its quantitative characteristics are too variable in space (from lake to lake) and in time to assume the existence of constants and quantitative laws. These laws are at least not obvious and may be hardly elucidated by simple regressions.

Certainly, there are ecological problems, for which solving the balance approach is of little use. These problems lie in the sphere of *population analysis* (see Caughley 1977, Krebs 1985) aimed at revealing factors and mechanisms of alterations in the abundance of population in space and time (just temporal aspect will be considered here in more details). The main difference between population analysis and balance approach consists in the rejection of nomothetic paradigm by the former method. Rather tough and stable pattern of energy and matter flows between compartments of ecosystem is replaced here by a far less solid, changeable temporally and spatially net of causes and effects, by system of interspecific relations under conditions of particular environment.

Although this picture is sufficiently certain in each given place (lake or other water body) and at each given time (not too long interval) to be revealed and quantitatively characterized (Ivlev 1945), it does not lead to revealing the universal laws and stable system of ratios. Therefore, the population analysis does not search for general laws but only for explanations of particular situations. The only thing which is suggested to be universal is the sum of methods and principles used to search for such explanations. These principles comprising the essence of the population analysis research program are the following: 1) to study particular processes occurring in the populations rather than their states averaged in time; 2) to study processes at time scale which is appropriate to rates of these processes; 3) to reveal the mechanism (or the chain of causes and effects) relating the influence of an environmental factor to the changes in population abundance; 4) to study the population characteristics as responses to influence of particular environmental factors.

The first principle means the rejection of averaging paradigm of the balance approach.

The second one shows how this rejection is practically achieved, i.e. by sufficiently frequent sampling and sufficiently experiments.

The third principle reflects the very essence of population analysis requiring to reveal the complex and variable pattern of factors which affect the population. It is not reduced to simple explanations such as "the increase in nutrient loading caused the increase in primary production" or "the population density increased because the temperature has risen". Such explanations are insufficient and, therefore, not always correct since the evaluations of particular factors are often very approximate, and, due to the emphasis on some factors taken into account in given work (because they are easily measured), they lead to the underestimation of other factors which have really caused the changes observed. Real situation may be completely different. Actually, if one can observe more consequences of given factor influences, and more

intermediate links in the cause-effect chain, the more solid is the statement that just change in this factor led to observed alteration in species abundance (Polishchuk 1986). The methodology of constructing the causal chains is being developed also in current investigations of population dynamics of insects (Sharov 1989).

Finally, the fourth principle indicates how to construct the causal chains and to reveal the mechanisms which are considered by the third principle. In short, it requires to make a start from population, and then to move step by step to environmental factors which were supposed to be responsible for consequent changes. In other words, such approach implies the way from effects to causes but not in the opposite direction. The traditional way, from causes to effects, is apparently less effective since, strictly speaking, it requires a successive looking over all the possible causes. At the same time, the success of movement from effects to causes depends on whether we possess all necessary data on population attributes, the change of which unambiguously depends on certain external influences. A search for such attributes somewhat resembles the search for stable relations between ecosystem variables treated by the production approach in aquatic ecology, but in the case of population analysis investigators assume only qualitative approximate correspondence, suggest the influence of several rather than a single factor and come to final conclusions only after consideration of all these attributes.

The application of these principles may be illustrated by the study of population abundance dynamics of the cladoceran *Daphnia galeata* in the Mozhajsk Reservoir in summer 1985 (Polishchuk and Sakharova 1987, 1988).

Natality and mortality are the direct causes determining the temporal change in population abundance. To make a start "from the population" in search for factors of dynamics (the fourth principle), it is neccessary to be able to estimate the birth and death rates. The methods used to evaluate these characteristics for the planktonic animals are well known (Polishchuk 1986, Gabriel et al. 1987, Voronov 1991). In particular, it was shown that the precision of estimating the birth and death rates considerably depends on the interval between samplings being the highest when the interval is equal to the duration of egg development. At usual summer temperature, this interval comprises about 3-4 days; this circumstance forces to take samples rather frequently (the second principle).

Using the samples taken every 3-4th day, we calculated the birth and death rates in *Daphnia* population. It was found that during the first half of summer the values of these parameters were out of phase resulting in fluctuations in abundance; on the contrary, during the second half of summer the birth and death rates were in phase, so that, abundance maintained at the constant level. Thus it may be suggested that the mechanism of regulation of the abundance was different in different summer periods.

The next step of this analysis was connected with a search for factors responsible for changes in birth and death rates each considered separately. From the equation used to estimate the birth rate follows that there are only three intrapopulation factors determining the birth rate, namely, duration of egg development, fecundity, and percentage of adults in total numbers of *Daphnia*. A method has been proposed for estimating contributions of these factors into the change of birth rate in each time interval between consequent samplings (Polishchuk and Sakharova 1987). It was found that these contributions did not remain constant but showed seasonal changes. Some kind of "play" of factors occurs in each time interval, and the factor that has changed to a greater degree in comparison with two others "leads" the birth rate. In our example, the fecundity was such a leading factor in those intervals when the birth rate was changed (increased or decreased) considerably. As the fecundity is determined mainly by trophic conditions, we can construct the following causal chain: trophic conditions — fecundity — birth rate — abundance. Tracing of this chain illustrates the third principle while the connection with trophic conditions via birth rate and fecundity illustrates the fourth principle, though the role of trophic conditions is still supposed rather than proved.

Another important population attribute is the average growth rate of individuals. As it was established in our example (Polishchuk and Sakharova 1988), the growth rate of young, immature cladocerans may be changed 2-4 times within 5-7 days. Such rapid change in the growth rate determines a necessary frequency of its experimental evaluation (the second principle). Comparison of the seasonal dynamics of young cladoceran growth rate with the dynamics of fecundity of adults showed that they were changed synchronously all over the summer. We want to emphasize that fecundity was measured in field samples while the growth rate was estimated in specially conducted laboratory experiments. The temperature showed insignificant seasonal variability and therefore practically could not determine the changes in growth rate of individuals. Thus the seasonal dynamics of fecundity and that of individual growth rate

can be considered as different reflections of one and the same factor, this factor being the trophic conditions in the lake. This is a good illustration of the fact that the more population characteristics are estimated, the better grounded are our ideas on environmental factors affecting the population (the third principle).

The cause-effect chain discussed above resulted in change of abundance by means of the birth rate. The second line of causal relations goes to the explanation of mortality dynamics. Unfortunately, the population analysis was not too successful in the study of the mortality factors. This is connected both with the fact that the death rate is estimated with a greater error than the birth rate (by difference between the birth rate and the rate of abundance changes), and the fact that it is difficult to find population characteristics which may directly indicate the mortality factors and in the same time be measurable in nature. One of such characteristics is the ratio between the death rates of young and adult individuals, which may be calculated if one knows the production value (Polishchuk 1990). Since, in planktonic crustaceans, the press of invertebrate predators affects mainly juveniles while that of vertebrate predators (fish) affects adults, the above-mentioned ratio may serve as an indirect index of influence of one or another predator groups.

Explanations given at the population level are necessary and possible, being found not only under conditions of specially simplified laboratory experiments but also in nature. Sequences of causes and effects, determining the alterations in abundance, comprise the interacting causal chains, some kind of a "causal net" (a simple example of such a net is the simultaneous influence of trophic conditions on the fecundity and the growth rate in *Daphnia*). Nevertheless, it is possible to isolate one or several main (though, probably, rather generalized) factors among multitude of others that may influence the population, and to estimate their contribution into the regulation of abundance. Quantitative "laws of abundance regulation" may hardly be obtained this way, although, probably, there is a limited number of qualitative patterns of such regulation. Therefore the aim is not to search for "laws" (which are likely absent) but to develop a sufficiently universal technology ("know how") of searching for causal mechanisms applicable to various populations and various habitats. Solution of this problem will clear the way to the development of simulation models based on qualitative conceptions of key factors the role of which was preliminarily estimated in the analysis of particular population. These models, as intermediate ones in their level of complexity between the model of "careful wisdom" (the complete account for all the ecological variables) and the model of "resolute dilettantism" (the more or less arbitrary selection of only some of them) (Sukhanov et al. 1990), will be probably more effective than others.

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Популяционный анализ и продукционный подход — два облика современной гидробиологии

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РЕЗЮМЕ. Обсуждены основные черты двух исследовательских программ, сосуществующих в современной гидробиологии: продукционно-энергетической и популяционно-аналитической. Первая исходит из того, что между элементами экосистемы существует достаточно жесткая система функциональных связей и, соответственно, зная величины одних переменных, можно рассчитать значения остальных. Таким образом, неявно подразумевается наличие экологических констант, или, что тоже самое, устойчивых соотношений между экологическими характеристиками (экологических "законов"). Другая особенность продукционно-энергетической программы — перенос экологических характеристик одних экосистем на другие (например, при расчете регрессионных зависимостей для совокупности озер). Данному подходу свойственно также оперирование только с усредненными характеристиками и рассматривание трофических уровней в качестве основных взаимодействующих элементов. Популяционно-аналитическая программа ищет не общие законы, а объяснения конкретных ситуаций, стремясь выявить факторы и механизмы, ответственные за изменение обилия популяций во времени и пространстве. Универсальными предполагаются только методы или принципы поиска объяснений конкретных ситуаций. Основные принципы популяционного анализа: 1. изучать не усредненные во времени состояния популяции, а протекающие в ней процессы; 2. изучать процессы на временах, адекватных скоростям их протекания; 3. выявлять механизмы связи между воздействием того или иного фактора среды и изменением численности, выстраивая причинную цепь взаимосвязей; 4. изучать специфику реакции популяционных характеристик на воздействие определенных средовых факторов и на этой основе выносить суждения о самих этих факторах.